ISSN 0889-3667
JCPB 5(1)1-46(1991)

INTERNATIONAL JOURNAL OF COMPARATIVE PSYCHOLOGY

Volume 5, Number 1, Fall 1991

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Subscription rates:

Volume 5, 1991–1992 (4 issues) $95.00 (outside the U.S., $110.00). Price for individual subscribers certifying that the journal is for their personal use, $36.00 (outside the U.S., $45.00). Members of the International Society for Comparative Psychology receive their yearly subscription at the rate of $27.00 as part of their membership dues (sliding scale). For membership information, write to Dr. Sally A. McFadden, Secretary-Treasurer, Department of Psychology, University of New Castle, New Castle NSW, 2308, Australia; bitnet address: PSSAM@cc.newcastle.edu.au or Fax 61 49 216 902.

INDEXED OR ABSTRACTED IN: Psychological Abstracts.

ISSN 0889-3667 IJCPE8 5(1)1–46(1991)

International Journal of Comparative Psychology, Vol. 5, No. 1, 1991

ACQUISITION OF PINE CONE STRIPPING BEHAVIOUR IN BLACK RATS (*Rattus rattus*)

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ABSTRACT: Black rats (*Rattus rattus*) have begun occupying a new habitat in recent years—the Jerusalem pine (*Pinus halepensis*) forests in Israel. In this, otherwise almost sterile habitat, the sole source of nourishment for the rats is the pine seeds that can only be extracted from the cones through a complex feeding technique. Adult black rats unfamiliar with the technique (termed "naive") were unable to attain it either through trial and error or through observational learning when housed with experienced rats (termed "strippers"). In contrast, black rat pups raised by stripper mothers did learn the pine cone opening behaviour. In addition to the presence of a stripper model, however, the clues of the pine seeds themselves, as well as partially open cones, may also play a role in the acquisition of the technique. The state of the cone itself, when encountered by the rat pups, may be an important factor. Three groups of experimental animals were used: 25 pups born to naive mothers and reared on rat chow without exposure to either stripping mothers or partially opened cones; 25 pups born to naive mothers and exposed to pine cones in various stages of opening; 55 pups born to stripper mothers and exposed both to pine cones and to the presence of their mothers actively involved in stripping the cones and feeding on the seeds. We found that pine cone stripping behaviour is learned through two stages of a local enhancement effect: First, the pups are directed to the pine cones as a food resource, and then to the cone's proximal end as a starting point. The development of the stripping technique is acquired individually, with accumulating experience.

Black rats (*Rattus rattus*) have begun occupying a new habitat in recent years—the Jerusalem pine (*Pinus halepensis*) forests in Israel. In this, otherwise almost sterile habitat, the sole source of nourishment for the rats is the pine seeds that can only be extracted from the cones through a complex feeding technique. The scales must be stripped from the cone in a sequential fashion in order to expose the underlying seeds, which are tightly organized around the shaft of the cone. The rat systematically strips the scales one by one, following the spiral order around the shaft, until only the bare shaft remains (Aisner & Terkel, 1985).

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A series of experiments revealed that adult black rats unfamiliar with the technique (termed "naive") were unable to attain it either through trial and error or through observational learning when housed with experienced rats (termed "strippers"). In contrast, black rat pups raised by stripper mothers did learn the pine cone opening behaviour. Cross-fostering pups born to naive mothers on stripper mothers, and vice versa, demonstrated that the pine cone opening technique is probably acquired through a process of cultural transmission rather than genetically (Aisner & Terkel, 1985, 1991).

In addition to the presence of a stripper model, however, the clues of the pine seeds themselves, as well as partially open cones, may also play a role in the acquisition of the technique. As the state of the cone itself, when encountered by the rat pups, may be an important factor, this study was aimed at determining the influence of various stages of stripped cones on the learning process undergone by black rat pups lacking a stripper model.

METHODS

Three groups of experimental animals were used. Group 1 comprised pups born to naive mothers and reared on rat chow without exposure to either stripping mothers or partially opened cones; Group 2 comprised pups born to naive mothers and exposed to pine cones in various stages of opening; while Group 3 was comprised of pups born to stripper mothers and exposed both to pine cones and to the presence of their mothers actively involved in stripping the cones and feeding on the seeds. All pups were kept with their dams until approximately 80 days of age, at which time they were tested for their ability to strip cones.

ANIMALS AND PROCEDURES

In the first and second groups, the mothers (n = 5 in each group) were naive laboratory rats that had never been exposed to pine cones. Each dam raised 5 pups, housed in 35 × 50 × 35 cm glass terraria, with wire mesh lids. In the first group, the pups were exposed only to rat chow and had no experience with pine cones.

In the second group, each terrarium was divided in half by a wire mesh partition with an opening (2.0 cm × 2.0 cm) large enough to permit the pups, but not the mother, to cross through the divider. Rat chow powder (Lavena, Asia & Maabarot) was available for 3 hr daily and water was supplied ad libitum. Mother and litter were housed in one half of the terrarium, and a fresh batch of eight pine cones was placed each day in the other half, with the previous batch being removed. The cones were at four different stripped stages: 2 closed; 2 stripped of scales only at the proximal end; 2 half stripped of scales; and 2 bare shafts, stripped of all

scales but still containing a few uncollected seeds. The cones had been stripped by stripper rats from other cages in our rat colony, so it is possible that the pups could have been attracted to them by the residual odour of conspecifics (Galef, 1982). Since rat chow was restricted to 3 hours daily, the pups were motivated to search for an additional source of food, and they became interested in the pine cones which had been placed in the other half of the cage.

In both Groups 1 and 2, when the pups reached 80 days of age, the mother was removed from the cage and the pups were tested for 21 days to determine their ability to strip cones. Because of the natural timidity of the wild rats, they only rarely open pine cones in the presence of an observer. Thus their ability to open and strip cones was determined indirectly by examining the state of the cones and observing the physical condition of the tested pups, which is very clearly reflected in the appearance of their dark fur; after two days of food deprivation it becomes clumped and matted. Rats that did not strip cones during the test by the second day were defined as nonlearners and were removed from the test cages and fed rat chow. Because of the structure of the cone, in which the rigid scales overlap and tightly cover the seeds, there is no way in which the rat can obtain the seeds without an efficient method of stripping the cone. Successful cone opening was defined as the ability of the rats to strip intact pine cones, leaving only the bare shaft, and obtain the seeds within as a sole source of nourishment, while maintaining normal physical condition.

Group 3 comprised 10 adult stripper female rats which raised a total of 55 pups (3–7 pups/litter). These females were experienced in stripping cones and efficiently obtaining the seeds. The pups in this group were therefore exposed both to their mothers' opening the cones and to the cones themselves in various stages of having been stripped. At the age of 60–80 days, the pups were tested as in Groups 1 and 2 for their ability to open the cones.

RESULTS

Results (Table 1) indicate that none of the pups from the first group, which had no experience with pine cones, knew how to open cones. One quarter (24%) of the pups from the second group did learn the pine cone stripping technique without having observed the behaviour from a model. Despite the lack of imitation involved in acquiring the pine cone opening behaviour, the presence of a stripper mother did facilitate learning by the pups. Two thirds (65.5%) of the pups learned the stripping technique when reared with a stripper mother for 60–70 days, compared with pups which were reared for 80 days with the stripping products only. When the data were transformed (arc sin) to adjust to normal distribution, a t test was significant ($p < .05$; Table 1).

TABLE 1
Effect of Various Raising Conditions on Pine Cone Opening Behaviour in Black Rats

Group	*No. of pups*	*No. of pups learning to open cones*	*%*
1. Pups exposed only to rat chow	25	0	0
2. Pups exposed only to pine cones	25	5	24
3. Pups exposed to pine cones and stripper mother model	55	36	65.5

DISCUSSION

The spread of the phenomenon of milk bottle opening by tits was originally reported by Fisher and Hinde (1949) and interpreted as resulting from interaction of naive birds with birds experienced in milk bottle opening (Hinde & Fisher, 1972). Although the authors emphasized that both social and nonsocial factors were involved in the spread of this behaviour, they did not uncover the mechanism by which it was acquired. Sherry and Galef (1984, 1990) show that providing birds with the experience of encountering previously opened bottles is in itself sufficient to establish the bottle opening behaviour, and thus conclude that such habits can be transmitted without involving social components.

In our own experiments too, 24% of the rat pups did learn to strip the cones when supplied only with the nonsocial component: i.e., pine cones in various stages of opening. Perhaps because of the structure of the pine cone, the partially opened cone might be the crucial factor in the learning process. The seeds in the cone are covered by hard, rigid scales, tightly overlapping around the shaft of the cone. Starting from the base, each row of scales covers the row above. The key to stripping the cone efficiently is to start at the base and systematically remove the scales in spiral order around the shaft. An already started cone may thus provide the rat pup with the correct stimulus to learning the stripping technique. Although one quarter of the pups learned to strip cones when supplied only with the nonsocial component (the cone itself), the addition of the social influence (a "stripping" model) significantly increased the proportion of pups that acquired the technique to two thirds.

The presence of a stripper mother can facilitate learning in several ways. At the time that the pups start to leave the nest and eat solid food, new behaviours such as licking and sniffing the mother's mouth appear (Ewer, 1971). While the mother is actively opening the cones, stripping

the scales and exposing the seeds to feed on them, the developing young gather round her mouth and attempt, with partial success, to obtain some seeds. At a later stage of development the pups attempt to snatch cones from the mother while she is stripping them, and they then continue the stripping process. Kemble (1984) described similar behaviours which facilitated the learning of cricket predation by northern grasshopper mouse pups (*Onychomys leucogaster*).

Food preferences of young rats have been shown to be strongly affected by the presence of adults eating near a food source (Galef, 1982). This could facilitate learning to strip pine cones by pups reared with stripper mothers. Moreover, chemical cues also act as an important stimulus for food preferences in rats (Galef, 1982), and a mother's odour on a stripped cone may provide a stronger stimulus to investigate the cone than the odour of a strange rat.

We proposed that pine cone stripping behaviour is learned through two stages of a local enhancement effect as suggested by Thorpe (1956): First, the pups are directed to the pine cones as a food resource, and then to the cone's proximal end as a starting point. The development of the stripping technique is acquired individually, with accumulating experience.

ACKNOWLEDGEMENTS

The authors are grateful to Ms. N. Paz for preparing and editing the manuscript, and to Dr. D. Goulet for his reading of an earlier version. We would like to thank Professor J. Galef for his valuable suggestion to provide already started cones as a clue for the rat pups. The research was partially supported by National Geographic Society grant #3084-85.

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International Journal of Comparative Psychology, Vol. 5, No. 1, 1991

DISCRIMINATION OF MUSICAL STIMULI BY RATS (*Rattus norvegicus*)

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ABSTRACT: Rats were trained under go–no go conditions to discriminate among complex acoustic stimuli (short musical sequences). In order to investigate the role of different stimulus attributes in discriminative performance, two short musical excerpts differing in their melodic pattern, but maintaining the number, pitch, and duration of notes constant were provided in two different timbres, to obtain four different complex auditory stimuli. According to the experimental condition, the discriminative stimuli were, therefore, different in structure, in timbre or in both aspects.

The animals were able to discriminate efficiently among the musical sequences only when cues furnished by timbre were available, whereas melodic differences made no difference. In the experimental setting used, the rat's discrimination of complex auditory stimuli appears, therefore, to be based neither on the melody nor on a compound of melody and timbre, but simply on the properties of the timbre of the stimuli.

RIASSUNTO: Dei ratti sono stati addestrati con una procedura go–no go a discriminare tra stimoli acustici complessi (brevi brani musicali). Al fine di valutare il ruolo di attributi diversi di uno stimolo complesso nell'acquisizione di una discriminazione condizionata, sono stati sintetizzati su personal computer due brevi brani musicali, identici nel numero di note costituenti, nella frequenza media, nella durata e nel ritmo, ma sensibilmente diversi sotto l'aspetto melodico. Le due melodie sono state poi realizzate in due diversi timbri "strumentali" in modo da ottenere quattro diversi stimoli complessi. A seconda della condizione sperimentale, gli stimoli discriminativi differivano o per le loro caratteristiche melodiche, o per quelle timbriche, o per entrambi questi aspetti.

I risultati ottenuti indicano che, nella situazione sperimentale da noi utilizzata, i ratti sono in grado di discriminare tra stimoli acustici relativamente complessi, ma suggeriscono che la discriminazione non è basata tanto sulla struttura melodica quanto sulle caratteristiche timbriche dello stimolo utilizzato.

INTRODUCTION

Although most studies of conditioned discrimination learning and of stimulus control in animals have been carried out with simple stimuli such as colored lights or tones of different intensity or pitch, a growing body of ethological data gathered both in the laboratory and in the field

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and derived mainly from studies on animal communication point out that for many species of birds and mammals the stimuli controlling behavior are often quite complex, and that animals are endowed with sophisticated abilities for their recognition (Cheney & Seyfarth, 1980, 1988; Falls, Dickinson, & Krebs, 1990; Falls, Horn, & Dickinson, 1988; Harrington, 1986).

Moreover, the recent and increasing interest in cognitive processes in animals (Hulse, Fowler, & Honig, 1978; Roitblat, Bever, & Terrace, 1984; Weiskrantz, 1988) makes it necessary to devise more complex experimental situations, better suited to investigate the integration of complex information. A number of studies have recently been performed in such a cognitive framework using complex visual stimuli varying along several dimensions at the same time. For example, natural-concept discrimination in pigeons has been investigated using photographs representing open-ended categories such as people, individual persons, alphanumeric characters, fishes, etc. (Herrnstein, 1984; Honig and Stewart, 1988 and Wilkie, Willson, and Kardal, 1989). Others have shown that nonhuman primates can acquire high-order abstract visual concepts (Schrier, Angarella, & Povar, 1984; Schrier & Brady, 1987; Rosenfeld & Van Hoesen, 1979; Yoshikubo, 1985).

Laboratory studies based on complex acoustic stimuli have been less frequent, but some interesting studies have been performed to assess the way animals analyze complex auditory information. It has been shown that both birds and mammals can be trained to discriminate synthetic and naturally produced speech stimuli (Hienz, Sachs, & Sinnott, 1981; Kluender, Diehl, & Killeen, 1987; Kuhl, 1981, 1986; Kuhl & Miller, 1975, 1978; Waters & Wilson, 1976), thus suggesting that the perception of speech sounds is not necessarily a uniquely human ability. A number of studies showed that starlings and other songbirds can manage structured information and respond differentially to organized computer generated sequences of tones (Hulse, Cynx, & Humpal, 1984a,b, 1985; Hulse & Cynx, 1985, 1986). Shy, McGregor, and Krebs (1986) using operant techniques demonstrated that great tits categorize natural song types in the same way as humans do, at least to some extent.

There is evidence that, despite a rich vocal communication system, primates are much more efficient in acquiring visual than auditory discriminations (Segal & Harrison, 1978; Thompson, 1980). It has been suggested that this reduced discriminative ability might be related to the very limited patterning of the stimuli employed in most studies (Beecher, Petersen, Zoloth, Moody, & Stebbins 1979). Primates would not attend to unpatterned sounds, usually unimportant in their natural habitats. To test this hypothesis, D'Amato and Salmon (1982) trained both monkeys (*Cebus apella*) and rats to a similar auditory discrimination task, where S+ was a short and very simple computer generated structured six-note melody, while S− was a simple "glissando." Both

stimuli were presented for a very short time (slightly more than one second). Although all the primtes eventually learned the task, they always proved markedly less efficient than the rats, which were consistently faster in learning the auditory discrimination and more efficient in generalizing it to other stimuli. Moreover, the performance of the rats was very poor when the discriminative stimuli were constant tones rather than interrupted tones or patterned melodies. These experiments seemed, therefore, to confirm the importance of auditory stimulus patterning for both rats and primates.

However, in a later study with a different setup, the same authors (D'Amato & Salmon, 1984) found that neither rats nor monkeys appeared to make great use of structural cues, but seemed to base their discriminations on more local aspects of the stimuli, such as overall frequency differences. They concluded that the ability of the rats and monkeys to discriminate between patterned auditory stimuli displayed in their previous study had been overestimated. The local feature responsible for discrimination learning in the 1982 paper was apparently the frequency of the initial notes of the melody.

On the other hand, Porter and Neuringer (1984) have argued that their pigeons were not only able to discriminate among complex melodic patterns, but also skillful in generalizing to other stylistically similar musical pieces in almost the same way as people do. To rule out the possibility that the rats would respond to some simple attribute to the stimuli, they employed long and complex musical excerpts: The stimuli differed, therefore, along several dimensions, pertaining, for example, to instrumentation, tempo, timbre, richness of sound, pitch, etc. As the exact nature of the music varied considerably from trial to trial, Porter and Neuringer (1984) concluded that pigeons were attending to some rather complex attribute of the musical stimuli. However, the stimuli employed in the study were extremely complex and it was, therefore, impossible to tell which auditory cue or pattern of cues was responsible for the results.

These findings clearly show that nonhuman animal responses to auditory events may be more complex than is usually assumed, and suggest that at least some species can respond to the pattern of the acoustical stimuli rather than to limited local features. However, without a complete and detailed analysis of the controlling features of the acoustic signals, either natural or artificial, this latter possibility cannot be ruled out. In particular, the possibility that discriminative behaviour could be based on the complex stimulus "in toto" rather than on other structural elements (i.e., rhythmic, tonal or timbric patterns) has not been fully investigated.

The aim of the present study was to extend D'Amato and Salmon's study of rats to a more complex auditory domain. By the use of forward and backward versions of a short melody, we were able to keep constant both the rhythmic patterns and the mean frequencies of the two tunes.

Our situation was in this respect somewhat similar to the one used by D'Amato and Salmon (1984). Furthermore, to allow for a meaningful patterning of the melody, we chose a longer lasting melody. Finally, to avoid the possibility pointed out by D'Amato and Salmon (1984) that the discrimination would be based on the frequency of the initial notes, in our study the onset of the stimulus presentation was randomly chosen at different points of the melody. The purpose of the experiment was, therefore, first, to ascertain whether rats would acquire an operant discrimination based on relatively complex and structured musical sequences and, second, if they succeeded in doing so, to evaluate whether the discrimination was based on the melody as a whole, or on other stimulus attributes, such as timbre.

METHOD

Rats

Twenty-four female Long-Evans rats, obtained from Charles River Inc. were studied. They were about five months old at the start of the study and had no previous experimental experience. During the experiment, they were housed in pairs in 56.5 × 35 × 18 cm plastic cages under an artificially reversed light cycle (light on from 9 p.m. to 9 a.m.). While dry food was constantly available in the home cages, water was available only for 1 hr after each daily session; therefore, all rats were water deprived for approximately 23 hr before each experimental session.

Apparatus

The apparatus used consisted of two Grason-Stadler operant chambers, housed in custom-built sound attenuating enclosures, each consisting of two laminated wood boxes one inside the other and separated by a 5 cm thick layer of expanded styrene. Each chamber measured 23 × 20 × 29 cm. The side walls of the chambers were clear Plexiglas; the front and the rear walls were aluminium; and the floor was formed of 3 mm steel bars. A response lever was located on the left side of the front panel, 8.5 cm from the grid floor, and extended 2 cm from the wall. Reinforcement consisted of .4 ml of water presented for 4 sec through a Gerbrands liquid dipper positioned in the middle of the lower part of the front wall.

Diffuse illumination was provided by a 25-W bulb positioned behind the front wall of the chamber. A Philips wide-range two-way speaker (model PRO 602 with a rated response of 20 to 20,000 Hz) was located 10 cm behind the front panel. The musical stimuli were presented with a Marantz/Superscope Model CD-330 tape recorder (rated frequency

FIGURE 1. Scores of the discriminative stimuli.

response 40 to 15,000 Hz ± 3 dB; S/N ratio with Dolby B on, 55 dB), and their intensity was held constant at approximately 85 dB throughout the experiment. All aspects of the experiment were controlled by conventional relay equipment.

The auditory stimuli were two 37-note tunes synthesized with the Instant Music program running on an Apple II GS personal computer. One of the tunes, referred to as Tune 1, was the well-known folk melody "Frère Jacques" while the other, Tune 2, was obtained by arranging the component notes of "Frère Jacques" in a reversed sequence without altering the rhythmic structure (the scores are presented in Fig. 1). The two tunes were therefore identical with respect to their mean frequency, note duration and rhythm, but noticeably different in their melodic patterns.

Both tunes were synthesized in two different "instrumental" timbres, namely trumpet and guitar, and recorded on cassettes. The three different experimental conditions were, therefore, characterized by differences in the melodic and timbre features of the tunes. In the *Timbre-Melody* condition, the two stimuli differed both in structure (sequence of the individual notes) and in timbre; in the *Melody* condition the sequence of the notes was different, but the timbre was maintained constant; in the *Timbre* condition the same sequence of notes was presented in the two different timbres; finally, the *Control* rats were always presented the same sequence of notes with the same timbre. In principle, there were 16 different possibilities (4 in each of the four conditions). However, for practical reasons, the study has been carried out with only four groups, each given one condition.

TABLE 1
Experimental Design and Discriminative Stimuli. Tune 1: Frère Jacques; Tune 2: Frère Jacques Reversed

	Timbre-Melody Condition (T-M group)	*Melody Condition (M group)*	*Timbre Condition (T group)*	*Control Condition (C group)*
S+	Tune 1	Tune 2	Tune 2	Tune 1
	Guitar	Guitar	Trumpet	Trumpet
S−	Tune 2	Tune 1	Tune 2	Tune 1
	Trumpet	Guitar	Guitar	Trumpet

Procedure

The animals were first magazine-trained and hand-shaped to press the lever on a continuous reinforcement schedule (CRF). After acquisition of the operant response, they were gradually introduced to a fixed-ratio 5 schedule of reinforcement (FR 5), that was maintained for a few sessions (2–4) in the absence of auditory stimuli.

The experiment was then carried out as follows:

Phase 1. After shaping was completed, a Mult. FR 5/Ext schedule was introduced. The subjects were then assigned at random to one of the four groups (Table 1). For the six rats in the TM group, the stimuli to be discriminated differed both in melody and in timbre. For those in the M group, S+ and S− differed in melody but were presented in the same timbre. For those in the T group, the only difference between S+ and S− was timbre. For the C group no acoustic discriminative information was available as the same tune (i.e., Tune 1, Trumpet) was played repeatedly in both contingencies. This group served to evaluate to what extent the behaviours of the experimental groups were controlled simply by fixed ratio schedule cues. The possibility of introducing a negative contingency during extinction was considered, but we decided that the advantages of such a procedure would have been overridden by its perturbing effect.

Acquisition training consisted of 50 consecutive daily sessions. Each session lasted 20 min and consisted of randomly intermixed 15 sec periods of either S+ or S−. The sequence of S+ and S− periods was randomized through a Campden Instrument random event generator so that in each session the average number of S+ equated that of S−. Therefore, the exact sequence of S+ and S− was unpredictable and varied from day to day. During each session the total number of responses emitted during S+ and S−, the number of S+ and S− presented, and the number of reinforcements obtained were recorded for each rat.

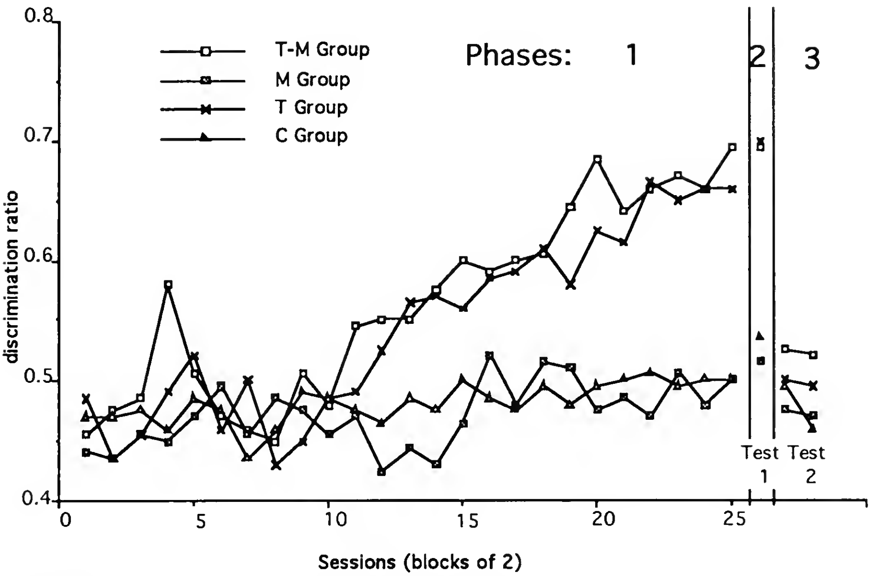

FIGURE 2. Performance curves for each group during the three phases.

Discriminative behavior was measured by a discrimination ratio (DR) defined by the following formula: $DR = R^+/(R^+ + R^-)$, *where:* $R^+ = Rs^+/S^+$ *and* $R^- = Rs^-/S^-$.

This formula was introduced to compensate for the effects of the variable number of stimuli introduced by the randomization over sessions of relatively short duration.

Phase 2. To test whether the regular alternation of the two stimuli and their longer duration affected the performance of the rats, Phase 1 was followed by two 20 min test sessions in which periods of S^+ and S^- lasting 1 min each were regularly alternated.

Phase 3. Four 20 min control sessions in the absence of the musical stimuli were performed to test whether to the discrimination obtained was based on the physical properties of the auditory stimuli or was due to some artifact. During these sessions blank tapes replaced the music, so that only an unstructured noise approaching white noise was presented, while all other contingencies were the same as during acquisition (Phase 1).

RESULTS

The main results of the experiment are reported in Fig. 2, showing for each group, in two session blocks, the mean discrimination ratios during the different phases. Table 2 reports the discrimination ratios of the

TABLE 2
Discrimination Ratios (2 Session Blocks) of Individuals in Each Group During Testing and at the End of Training (Last Four Sessions)

Session (Blocks)	Rat	Phase 1		Phase 2	Phase 3	
		47–48	*49–50*	*51–52*	*53–54*	*55–56*
T-M group	1	.56	.70	.67	.46	.54
	2	.57	.59	.66	.49	.48
	3	.63	.66	.66	.56	.57
	4	.75	.75	.74	.54	.57
	5	.71	.68	.74	.52	.46
	6	.70	.77	.75	.55	.50
M group	1	.47	.43	.57	.46	.48
	2	.49	.49	.50	.48	.45
	3	.40	.45	.42	.43	.41
	4	.51	.55	.56	.53	.52
	5	.47	.56	.61	.53	.57
	6	.43	.51	.47	.41	.42
T group	1	.73	.70	.69	.51	.51
	2	.69	.72	.71	.50	.50
	3	.54	.56	.62	.45	.40
	4	.60	.57	.68	.46	.53
	5	.64	.68	.65	.54	.44
	6	.74	.74	.79	.55	.54
C group	1	.53	.58	.59	.44	.42
	2	.51	.56	.58	.57	.51
	3	.53	.46	.53	.43	.52
	4	.42	.43	.48	.43	.43
	5	.52	.48	.49	.51	.42
	6	.48	.48	.52	.52	.47

individual rats of each group at the end of training (sessions 47–50) and during testing.

These results clearly indicate a difference in discriminative performance between the two groups that could make use of timbre differences (T-M and T) and both the M and the C groups. None of the rats in the last two groups showed any sign of learning the discrimination, whereas three of the six rats in the T-M and T groups were clearly responding above chance at the end of training (Table 2). The statistical significance of these differences in performance was assessed using a between subject two-way ANOVA based on the mean discrimination ratio of the indi-

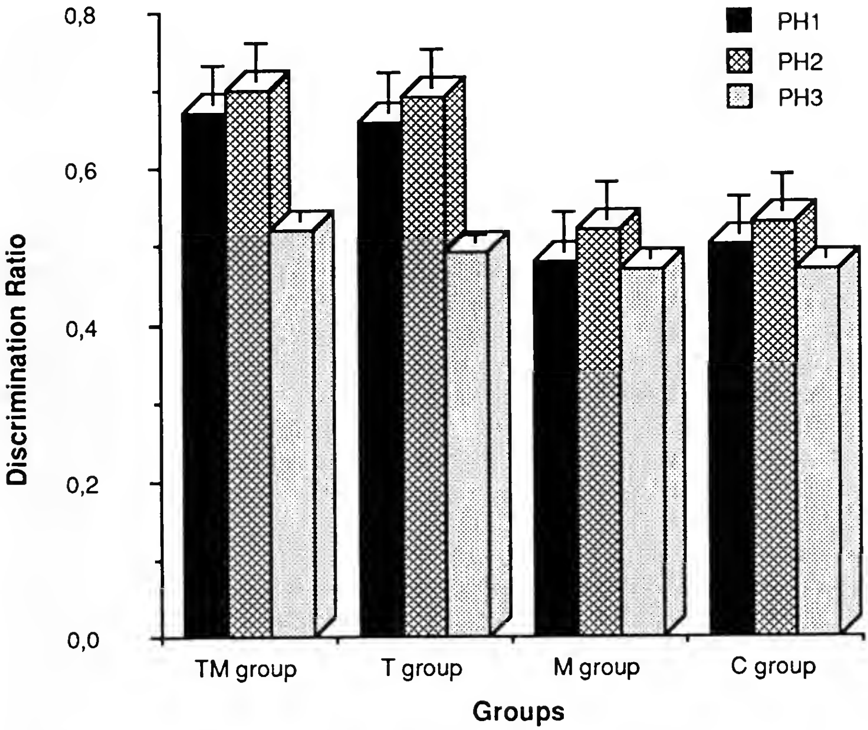

FIGURE 3. Mean discrimination ratios of the four groups in the last four sessions of Phase 1 and in Phases 2 and 3.

vidual subjects over the last four sessions of Phase 1. The test revealed a significant effect of timbre ($F(1, 20) = 43.503$, $p = .0001$), but not of melody or of timbre × melody interaction. These results seem to indicate that rats are able to discriminate among fairly complex artificial acoustic stimuli, but they also suggest that the discrimination is based on simple and general properties of the tune stimuli, such as timbre, rather than on the melodic structure.

The effect of Phase 2, consisting of the regular alternation of the two stimuli, was assessed with the Wilcoxon matched-pairs test, but no significant effect was revealed in any of the groups (for all of them, $p > .05$, two-tailed test).

However, when, in Phase 3, blank tapes were substituted for the musical stimuli, discriminative performance in the T-M and T groups was clearly disturbed (Figs. 2 and 3). The Wilcoxon matched-pairs test, employed to evaluate the effects of the withdrawal of the acoustic stimuli, showed no significant effects of this procedure, either in the C group ($p = .7$, two-tailed test) or in the M group ($p = .2$). Both the T-M and the

T groups showed a significant disruption of performance ($p = .02$), indicating that the discrimination was not an artifact but was really controlled by the experimental stimuli.

DISCUSSION

The results of the present experiment do, therefore, partly confirm those obtained in previous studies (D'Amato & Salmon, 1982, 1984), in that rats are shown to be able to discriminate among auditory stimuli more complex than those usually used in laboratory studies. Although the discrimination ratios reached by the T-M and T rats were relatively low in comparison with those reported by D'Amato and Salmon, due to the differences in procedure, exact comparisons are, however, difficult to make. The consistent differences in performance between the sessions, in which the musical stimuli were present (Phase 1) and the Control sessions (Phase 3) clearly indicate that discrimination was based on the musical stimuli.

As noted by D'Amato and Salmon (1982), rats are nocturnal animals and apparently rely more on olfactory and acoustic stimuli than on visual ones. It is, therefore, not surprising that they are able to respond appropriately to auditory stimuli of some complexity. Furthermore, these rodents make large use of infra- and ultra-sounds in their social interactions (Sales & Pye, 1974; Nyby & Whitney, 1978; Thomas & Barfield, 1985). The ability to efficiently analyze the auditory information in a large range of frequencies could at least partly explain this capacity. However, in the present study discriminative behaviour appears to be based more on general properties of the stimulus (i.e., timbre) rather than on its melodic pattern. This suggests that in the rat the recognition of complex auditory stimuli is based mainly on immediately detectable features, rather than on the detection of the structured organization of the stimulus. Although timbre is very complex to define from a physical point of view, it is usually quite easy to recognize, and is generally perceived as a "unitary" feature. On the other hand, the melodic structure is easily described in physical terms, but its apprehension as a structured whole may be less immediate.

The possibility that the differences in the performance of Melody and Timbre groups could be an artifact either of the particular samples of melody and timbre selected or of the procedure cannot be ruled out. Different melodic patterns or timbres and a different training procedure could conceivably have been more or less effective.

Moreover, the experimental stimuli used in this study were artificially synthesized and arguably devoid of any particular ecological meaning. It is possible that more natural and meaningful signals could have been discriminated more easily. As already suggested for other species (Marler,

1983; Snowdon, 1983), the possibility that the rat's ability to detect structural differences among complex auditory stimuli might be restricted to a limited range of biologically relevant acoustic signals needs further investigation.

ACKNOWLEDGEMENTS

This study was made possible by a grant from the Italian Research Council (C.N.R.).

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International Journal of Comparative Psychology, Vol. 5, No. 1, 1991

VARIATION IN THE AGGRESSIVE BEHAVIOR OF THE PARTHENOGENETIC LIZARD (*Cnemidophorus uniparens*, Teiidae)

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ABSTRACT: The desert-grassland whiptail (*Cnemidophorus uniparens*) is an all-female lizard species that reproduces clonally by parthenogenesis. Here we report marked geographic variation in the aggressive behavior of paired individuals in which pairs consisted either of individuals from within study sites or individuals representing each of two different study sites. Although we document allozyme variation within each study site, this did not differ significantly between sites. Previously reported restriction endonuclease analysis of mitochondrial DNA indicates that the two lizard populations used in the present study arose from the same or closely related maternal ancestors by interspecific hybridization. Gross climatological differences do not appear to explain the behavioral variation between sites. The possible roles of polygenic effects not detected by the biochemical analyses and laboratory studies of environmental effects on the development of aggressive behavior await further investigation.

Unisexual organisms provide an important model system that allows investigators to address persistent questions in behavioral biology in a novel way. To what extent is an individual's behavior shaped by its genotype versus its environment? How plastic are the responses of genotypes to environmental variation and how does genotypic plasticity vary among individuals? Reproduction by parthenogenesis is rare in vertebrates but relatively common in a few genera including the lizard genus *Cnemidophorus* (for an overview of unisexuality in vertebrates see Dawley, 1989 and Vrijenhoek, Dawley, Cole, & Bogart, 1989). Evidence

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from studies involving chromosomal and electrophoretic analysis indicates that the parthenogenetic *Cnemidophorus* sp. arose by hybridization (Dessauer & Cole, 1989). Some parthenogenetic *Cnemidophorus* sp. may have arisen from a single set of parents and are close to being genetically uniform (e.g., *C. neomexicanus,* Parker & Selander, 1984) whereas others may have arisen from multiple hybridization events and are quite diverse (e.g., *C. tesselatus,* Parker & Selander, 1976).

Several models have been proposed to describe variation in clonally reproducing species (Vrijenhoek, 1984). The frozen niche variation model proposes that diversity in clonal species arises primarily as a result of multiple hybridized zygotes from the same sexual ancestral species (Vrijenhoek, 1979, 1984) and is supported by a variety of field and laboratory data based on *Poeciliopsis* sp. fishes (Schenck & Vrijenhoek, 1989; Schultz & Fielding, 1989; Vrijenhoek, 1984, 1989; Wetherington, Schenck, & Vrijenhoek, 1989b; Wetherington, Weeks, Katora, & Vrijenhoek, 1989a). Secondarily, after one or more clones are produced by hybridization, recombination and/or mutation may produce additional variation within phyletic clones (Vrijenhoek, 1979). Thus, polyphyletic clones may be secondarily composed of cryptic clones or genotypically variable individuals having arisen from the same ancestral hybrid zygote. Although significant advances have been made in understanding the biology of clonally reproducing fishes, substantial deficits in understanding the biology of parthenogenetic lizards led Parker, Walker, and Paulissen (1989) to comment that "... the evolutionary study of cloned hybrid complexes of *Cnemidophorus* should serve as a guide to further genetic and/or morphological [we would add ecological, physiological and behavioral] study of contradictory cases rather than yielding robust conclusions of a mature theory."

Polyphyletic variation resulting from multiple hybrid origins and variation apparently from mutation or recombination have been documented for the *C. velox* complex, i.e., the named species *C. uniparens* and *C. velox* are both derived from the hybrid combination *C. burti* × *C. inornatus* × *C. inornatus.* Mitochondrial DNA analysis indicates that although *C. uniparens* and *C. velox* arose by hybridization involving the same species, the maternal ancestor of *C. uniparens* is *C. inornatus* and that of *C. velox* is *C. burti* (Moritz et al., 1989). Interestingly, *C. uniparens* and *C. velox* differ in several ways. *Cnemidophorus uniparens* inhabits desert grasslands south of the range of *C. velox* in Arizona, New Mexico, and Mexico. *Cnemidophorus velox* inhabits pinyon-juniper woodlands between 1,350–2,450 m associated with the Colorado Plateau in Colorado, Arizona, and New Mexico. Additional variation, apparently resulting from mutation and/or recombination has been reported in *C. uniparens* (Dessauer & Cole, 1986, 1989).

Although genetic variation for *C. uniparens* seems to be quite limited, there is considerable variation in aggressive dominance (Grassman &

Crews, 1987). Also, while collecting *C. uniparens* at two of our study sites for behavioral, reproductive and genetic studies (Moritz et al., 1989) we observed differences in average snout-to-vent length, minimum body size at which animals contained oviductal eggs, and the tendency of individuals to bite the fingers of their captors (unpublished field observations). Ecological studies of *C. uniparens* near Rodeo, New Mexico (Hulse, 1981), and our records based on hundreds of individuals collected over a 5-year period, indicate that these animals are phenotypically different from some *C. uniparens* collected near Willcox, Arizona. Rodeo and Willcox are approximately 121 km apart and separated by the Chiricahua Mountains. Near Rodeo, the smallest individual with either vitellogenic follicles or oviductal eggs ever recorded was 59 mm SVL (snout–vent length). Near Willcox, the smallest animal to date to have either vitellogenic follicles or oviductal eggs was 54 mm SVL. This reported variation in behavior and geographical differences in minimum body size at first clutch raise some interesting questions. For example, do individuals from near Willcox differ from those from near Rodeo in terms of other phenotypic characteristics such as aggressive and dominance behavior? Are differences between these populations a result of multiple independent origins for *C. uniparens* and can individuals from some populations dominate others with different parental origins?

The impetus for the present study was to document geographic variation in aggressive behavior between *C. uniparens* captured near Willcox and Rodeo, and to determine whether these two study populations are different phyletic clones based on mtDNA (Moritz et al., 1989) and allozyme analyses. Also, these populations were compared using protein electrophoresis and restriction endonuclease analyses of mtDNA (Densmore, Moritz, Wright, & Brown, 1989; Moritz et al., 1989; Moritz, personal communication). Here the purpose was to determine whether geographic variation in behavior was correlated with genetic diversity as estimated using state of the art biochemical methods. To determine whether environment might explain the geographic variation in behavior, average annual temperatures and precipitation covering 36 years, and average monthly temperatures (maximum, minimum, and mean) and precipitation for the 42 months prior to collecting the animals were compiled and analyzed for differences between the two study sites.

GENERAL METHODS

Animals

Populations of *C. uniparens* are found on the desert flats both east and west of the Chiricahua Mountains in southeastern Arizona (AZ) and southwestern New Mexico (NM). Our study sites were near Willcox, AZ and Rodeo, NM (121 km to the southeast of Willcox). Reproductively

mature *C. uniparens* were collected during the breeding season. Animals used in Experiments I and II were collected in June 1986. Experiment I was replicated with different animals collected in June 1987. Animals were collected using a portable drift fence, toe-clipped for permanent identification, returned to the Southwestern Research Station, American Museum of Natural History, where they were weighed, measured, palpated to determine reproductive condition, and housed until being transported to the University of Texas.

Housing and Maintenance

Animals were maintained in a computer-controlled environmental chamber. The microprocessor was programmed to simulate the changes in photoperiod, temperature, and humidity characteristic of southeastern AZ during the lizard's reproductive season based on weather data from previous years. The temperature was 27 °C at 0900 hr central standard time and gradually increased to 33 °C by 1200 hr where it remained until 1300 hr. For a complete description of animal capture and care see Moore, Whittier, and Crews (1984). Lizards were housed in 75 × 30 × 30 cm glass terraria with a 5 cm deep sand substrate. Three lizards all from the same collecting site were housed together in each terrarium. Radiant heat was provided by a 50-W heat lamp suspended 24 cm above the sand. In addition to the room lights, each cage received illumination from one General Electric ultraviolet light (F20T12/BL) and a Chroma 50 fluorescent light suspended 61 cm above the sand. Lizards were fed calcium and phosphate dusted crickets or mealworms three times weekly and were provided water in bowls ad libitum.

Quantification of Aggression

An ethogram for *C. uniparens* documenting aggressive behavior has been developed (Crews, Gustafson, & Tokarz, 1983), and agonistic encounters have been observed both in the laboratory (Crews et al., 1983; Gustafson & Crews, 1981) and field. *Cnemidophorus uniparens* will establish dominance hierarchies in the laboratory (Grassman & Crews, 1987; Gustafson & Crews, 1981).

In keeping with previous studies (Grassman & Crews, 1987; Gustafson & Crews, 1981), charges directed at cagemates were the behavior of interest. A charge was operationally defined as a rapid approach by one individual directed at another individual that resulted in the recipient either fleeing, chasing, or biting the instigator (Grassman & Crews, 1987). These encounters are often accompanied by other behaviors characteristic of aggression in *C. uniparens*: head nodding, bobbing, armwaving, and aggressive mouth gape (Crews et al., 1983; Gustafson & Crews, 1981).

All behavioral observations were made using a television camera and remote monitoring and recording systems. Observations were conducted between 1000 and 1300 hr, the lizards' period of peak activity in the field and laboratory. Lizards were observed for 30 min on each of 2 days. The test cage was a 75 × 30 × 30 cm glass terrarium divided in half with poster board. This formed two 37.5 × 30 × 30 cm test cages.

DESIGN OF BEHAVIORAL STUDIES

The intensity of aggression exhibited between individuals paired within inbred strains can differ from that in pairs comprised of individuals representing different strains (Bakker, 1986). Thus, separate experiments involving pairing animals within and between study sites were conducted.

Experiment I

In Experiment I, conducted in 1986 and replicated in 1987, a pair of lizards both from Willcox or Rodeo was placed in a test cage, and charges by each individual were recorded. Individuals forming the pairs had not been housed together previously. Pairs of lizards representing each site were observed simultaneously to eliminate temperature effects between sites. This experiment was designed to determine if there were differences in aggressiveness between Willcox pairs versus Rodeo pairs. The purpose of replicating Experiment I in 1987 with different individuals was to determine if differences in responses between populations were repeatable.

Animals collected from the Willcox study site are smaller in terms of average SVL compared to those from Rodeo (Grassman & Crews, unpublished data). Thus a sample of lizards from the Willcox population was naturally apt to be smaller in terms of SVL than a sample from Rodeo. This was not viewed as a problem with regard to interpreting behavioral differences between Willcox and Rodeo lizards for several reasons. First, two previous studies using *C. uniparens* demonstrated no relationship between SVL and aggressive dominance (Grassman & Crews, 1987; Gustafson & Crews, 1981). Second, in Experiment I the behavior of Willcox animals was independent of that for Rodeo animals. Third, size differences between the two populations could provide one explanation for any observed differences in aggression and could be examined further.

In Experiment I and the replicate experiment the pairs consisted of individuals from within the respective study sites; thus, this was a nested design. Observing each pair for 30 min on each of 2 days constituted two replicates for the nested design.

Experiment II

Experiment II involved pairs of lizards in which one individual from Willcox and one individual from Rodeo were placed in the test cage. This experiment was designed to determine if individuals from one population were dominant over those of the other population. Animals having similar SVLs were paired. Half of the Willcox animals in the Willcox–Rodeo pairs were larger than their cagemates and the Willcox animals were not significantly smaller than the Rodeo animals (Willcox, SVL = 62.9 ± 1.3, Rodeo, SVL = 64.4 ± 0.9; paired comparisons $t = 0.93$, df = 14, $p > .10$, 1-tailed, $p > .25$, 2-tailed). Thus, if SVL was an important variable behind differences observed in Experiment I, this effect would be eliminated from Experiment II. Alternatively, if SVL was not important the results of Experiment I should be corroborated by those of Experiment II. In Experiment II the 30 min observations made on 2 days were pooled. Pairs consisted of an individual from each study site; thus, this was a randomized blocks (paired comparisons) design.

Statistical Analysis of Behavior

Initially, data were analyzed using analysis of variance (ANOVA, Hicks, 1973). For each experiment geographic variation between study sites was the variable of interest. The pair effect was included in the models primarily to control variation and to account for the fact that behavior of individuals within pairs was not independent. Although animals from Willcox actively moved about in both experiments, few or no aggressive interactions were recorded and the data contained zero values. This raised concerns regarding the reliability of the tests of hypotheses. Therefore, assumption free bootstrap methods (Efron, 1982) were used to generate probability estimates (p') for comparison with the tabular p values. Briefly, this involved comparing F statistics generated using ANOVA performed on the observed data with the frequency distribution of F statistics generated by randomly sampling the data set with replacement and recalculating the ANOVA table (iterations = 10,000 for each experiment). The bootstrap likelihood for the observed outcomes (p') was estimated by comparing the observed F with the iteratively generated distributions of the F statistics. In all cases the tests of hypotheses based on bootstrap methods corroborated those based on tabular F statistics. The bootstrap estimates (p') are reported in Tables 1–3 for comparison with the tabular values.

GENETIC ANALYSIS

Although restriction endonuclease analysis of mtDNA did not distinguish *C. uniparens* collected near Willcox from those collected near

Rodeo (Densmore et al., 1989), protein electrophoretic analyses were performed to test the hypothesis that the two populations were genotypically distinct. The electrophoretic analysis was based on liver, muscle, and kidney extracts from 20 individuals each from the Rodeo and Willcox populations. Tissues were removed and stored in liquid nitrogen (−196 °C), and preparation and storage of tissue homogenates followed the protocol of Sites et al. (1988). The supernatant fractions of these homogenates were run on horizontal gels of starch (12.5%) containing equal parts of Sigma (lots 83F-0612, 44F-0619, 94F-0537) and electrostarch (lot 392).

Thirty-three enzyme systems encoded by 42 presumptive gene loci were resolved for both samples (Willcox and Rodeo). Enzymes used were as follows (Nomenclature follows recommendations of the Nomenclature Committee of the International Union of Biochemistry (1984). Suffixes "1" and "2" designate loci of multilocus systems in order of decreasing anodal mobility. Superscripts k, l, m refer to kidney, liver, and skeletal muscle, respectively): aconitate hydratase (Acon-1,2)^{l}, adenosine deaminase (Ada-A)^{k}, alcohol dehydrogenase (Adh-A)^{l}, aldehyde dehydrogenase (Aldh-A)^{l}, aspartate aminotransferase (Aat-1,2)^{l}, calcium-binding protein (Cbp-A)^{m}, creatine kinase (Ck-A)^{m}, dihydrolipoamide dehydrogenase (Dldh-A)^{l}, esterase (Est-1,2)^{l}, fructose biphosphotase (Fbp-A)^{l}, β-galactosidase (β-Gal-A)^{l}, general protein (GP-1,2)^{l}, glucose dehydrogenase (Gcdh-A)^{l}, glucose-6-phosphate dehydrogenase (G6pdh-A)^{l}, β-glucosidase (β-Gluc-A)^{l}, glycerate dehydrogenase (Glydh-A)^{l}, glycerol-3-phosphate dehydrogenase (G3dph-A)^{l}, hexokinase (Hk-A)^{l}, D-2-hydroxyacid dehydrogenase (2-Hadh-A)^{l}, L-iditol dehydrogenase (Iddh-A)^{l}, isocitrate dehydrogenase (Icdh-1,2)^{l}, L-lactate dehydrogenase (Ldh-A and Ldh-B)^{l}, malate dehydrogenase (Mdh-1,2)^{l}, malic enzyme (Me-1)^{l}, mannose phosphate isomerase (Mpi-A)^{l}, α-mannosidase (α-Mann-A)^{l}, peptidase (L-leucylglycylglycine) (Pep(lgg))^{l}, peptidase (phenylalanyl-L-proline) (Pep(pap))^{k}, phosphoglycerate kinase (Pgk-A)^{l}, phosphoglucomutase (Pgm-1,2)^{l}, phosphogluconate dehydrogenase (Pgdh-A)^{l}, superoxide dismutase (Sod-A)^{l}, uridine kinase (Uk-A)^{m}, xanthine dehydrogenase (Xdh-A)^{l}. Staining protocols were from Selander, Smith, Yang, Johnson, and Gentry (1971), Harris and Hopkinson (1976), and Richardson, Baverstock, and Adams (1986). Allozyme data were statistically summarized with the BIOSYS-1 program of Swofford and Selander (1981). Individual genotypes were used to calculate allele frequencies and the genetic distance coefficient (Hillis, 1984; Nei, 1978).

CLIMATOLOGICAL ANALYSIS

To test the hypothesis that climatic conditions differed between the Willcox and Rodeo study sites monthly averages of the high temperature, average daily temperature, low temperature, and precipitation for Jan-

TABLE 1
Experimental Design and Analysis of Variance Involving the Number of Charges Against Cagemates when *Cnemidophorus uniparens* from Two Study Sites, Willcox, AZ and Rodeo, NM, Were Paired with Individuals From Within Their Respective Localities (Animals Collected June 1986)

Site:	Willcox					Rodeo				
Pair:	1	2	3	4	5	6	7	8	9	10
Replicate 1:	0	0	0	0	0	17	0	38	8	36
2:	0	0	0	0	0	56	21	23	22	50

ANOVA:

Source	df	SS	MS	F	p'*
Site	1	3,672.05	3,672.05	28.48	0.001
Pair	8	1,549.40	193.68	1.50	0.250
Error	10	1,289.50	128.95		
Total	19	6,510.95			

*Bootstrap result. See the text for explanation.

uary 1983–June 1983 were statistically explored using ANOVA. *Cnemidophorus uniparens* individuals probably live a maximum of 3 or 4 years (Hulse, 1981). Additionally, annual average temperatures and precipitation for 1950–1986 were examined. Data were taken from National Oceanic and Atmospheric Administration summaries from stations closest to the study sites. For the monthly summaries data were for Willcox, AZ (8 km from the Willcox study site) and Animas, NM (20 km from the Rodeo study site) stations. With respect to the annual summaries, incomplete data were available for Rodeo, New Mexico (2 km from the Rodeo study site).

RESULTS

From a sample of 20 *C. uniparens* captured near Willcox, in 1987, four individuals smaller than 59 mm SVL were found to contain either vitellogenic follicles or oviductal eggs as determined by palpation. For Experiment I conducted in 1986, and for the replicate of the experiment conducted in 1987, Willcox lizards were significantly smaller than those from Rodeo (Willcox 1986, mean $\pm$ standard error SVL = 62.2 $\pm$ 1.4, Rodeo 1986, SVL = 65.9 $\pm$ 0.68, t = 2.26, df = 18, $p < .025$; Willcox 1987, SVL = 62.4 $\pm$ 1.0, Rodeo 1987, SVL = 69.2 $\pm$ 0.9, t = 5.04, df = 18, $p < .0005$).

TABLE 2
Experimental Design and Analysis of Variance Involving the Number of Charges Against Cagemates When *Cnemidophorus uniparens* from Two Study Sites, Willcox, AZ and Rodeo, NM, Were Paired with Individuals from Within Their Respective Localities (Replicate of the Experiment Outlined in Table 1 Using Animals Collected June 1987)

Site:	Willcox					Rodeo				
Pair:	1	2	3	4	5	6	7	8	9	10
Replicate 1:	0	0	0	0	0	20	43	13	6	43
2:	0	0	0	0	0	17	50	60	0	36

ANOVA:

Source	df	SS	MS	*F*	*p'**
Site	1	4,147.20	4,147.20	35.72	0.001
Pair	8	2,517.60	314.70	2.68	0.081
Error	10	1,176.00	117.60		
Total	19	7,840.80			

*Bootstrap result. See the text for explanation.

Behavioral Analysis

In Experiment I lizards in pairs consisting of two individuals from Rodeo charged each other more frequently than did lizards in pairs from Willcox (Table 1). Animals from Willcox exhibited no agonistic behavior. This finding was repeated in the replicate experiment with individuals from Rodeo charging each other more frequently than did lizards in pairs from Willcox (Table 2). Again, as in Experiment I, animals from Willcox exhibited no agonistic behavior. Pooling the data for Experiment I and the replicate experiment yielded a nonsignificant site by year interaction ($F(1,16) = .06$, $p = .8112$) indicating that the site effect was the same for both years. In Experiment I, variation comparing pairs nested within study sites was not significant (Table 1). In the replicate experiment variation comparing pairs nested within study sites was marginally nonsignificant (Table 2). Individuals from Rodeo charged each other an average of 54.6 (range 21–88) and 57.6 (range 6–93) times per hour in Experiment I and the replicate experiment, respectively. Also, there was a significant correlation in the number of charges between cagemates (one-tailed Spearman rank correlation $r = 0.59$, $p \leq .05$).

In Experiment II (one individual was from Willcox, and the other from Rodeo), lizards from Rodeo again charged more often than the lizards from Willcox (Table 3). One Willcox animal charged its Rodeo cagemate

TABLE 3
Experimental Design and Analysis of Variance Involving the Number of Charges Against Cagemates When *Cnemidophorus uniparens* from the Willcox, AZ Study Site Were Paired with Those from the Rodeo, NM Study Site (Animals Collected June 1986)

Pair (block):	1	2	3	4	5	6	7	8
Site								
Willcox, AZ	0	9	0	0	0	0	0	0
Rodeo, NM	4	21	28	9	0	6	6	3

ANOVA:

Source	df	SS	MS	F	p'*
Site	1	289.00	289.00	7.66	0.0095
Pair	7	468.72	66.96	1.78	0.1460
Error	7	264.00	37.71		
Total	15	1,021.75			

*Bootstrap result. See the text for explanation.

on its second day test. In each experiment individuals from both collecting sites actively moved about and approached each other. However, the individuals from Willcox (with the exception of the single animal in Experiment II) did not charge their cagemates. An average of only 9.6 (range 0–28) charges per hour by Rodeo animals was recorded.

Genetic Analysis

Twenty-seven of the 42 loci examined in samples from both sites were monomorphic for the same electromorph. A chi-square test of allele frequency heterogeneity between samples (Workman & Niswander, 1970) showed Pgdh-A to be the only locus with a significant intersample (Willcox vs. Rodeo) difference in allele frequency (chi-square = 8.06, df = 1, $p \leq .01$). Taken together, all variable loci showed no significant intersample allele frequency differences (chi-square = 15.20, df = 16, $p = .51$). The Nei (1978) genetic distance between these two samples was less than 0.01, and similar values were obtained for all other D estimates.

Individuals were delineated into eight genotypes (three collected from the Rodeo study area, and seven from the Willcox study area with two genotypes in common) on the basis of variation at six loci (Table 4). Representatives having the most common genotype accounted for 62% of the individuals collected and were found in samples from both field study areas (80% and 42% for Rodeo and Willcox, respectively). Representatives of the second most common genotype accounted for 18% of the individuals collected (10% and 26% for Rodeo and Willcox, respec-

TABLE 4
Eight Genotypes Based on Variation at Six Presumptive Loci for Triploid *Cnemidophorus uniparens* Collected Near Willcox, AZ and Rodeo, NM

	Enzymes					
Site (N)	*Pgdh-A*	*Dldh-A*	*Est-2*	*Fpb-A*	*aMann*	*Mdh-2*
Rodeo, NM						
(16)[a]	aaa	aaa	aaa	aaa	aaa	aaa
(2)[b]	abb	aaa	aaa	aaa	aaa	aaa
(2)	aaa	ab?	aaa	aaa	aaa	aaa
Willcox, AZ						
(8)[a]	aaa	aaa	aaa	aaa	aaa	aaa
(5)[b]	abb	aaa	aaa	aaa	aaa	aaa
(1)	bbb	aaa	aaa	aaa	aaa	aaa
(2)	abb	aaa	aaa	aaa	aaa	abb
(1)	aaa	aaa	abb	aaa	aaa	aaa
(1)*		aaa	aaa	aab	aaa	aaa
(1)*		aaa	aaa	aaa	abb	aaa
(1)* **		aaa	aaa	aaa	aaa	aaa

[a,b]Genotypes with the same superscripts are represented at both study sites.
*Pgdh-A was unresolved for these individuals.
**This individual is indistinguishable from genotypes varying only at Pgdh-A.

tively). The two remaining individuals from the Rodeo study area (10% of the Rodeo sample) represented a genotype unique to that site. Of the remaining seven individuals captured at the Willcox, AZ study area, two had the same genotype (11% of the Willcox sample), four other individuals each exhibited unique genotypes (each representing 6% of the Willcox sample) and one individual was unresolved for the Pgdh-A locus.

Climatological Analysis

The results concerning maximum, minimum, and average temperatures were similar and too extensive to detail; thus, only some general observations are presented here. For the years 1983–June 1986 Willcox was 0.72 °C warmer than Animas. For those years for which annual data were available, Willcox and Rodeo had the same average temperature (16.1 °C) while that of Animas was 15.5 °C. Although the 0.72 °C difference between Willcox and Animas was statistically significant, it does not seem that this difference alone could explain the behavioral differences observed. Most of the temperature difference was a result of higher winter temperatures in Willcox and there were significant month by site interactions. Stations did not differ in terms of precipitation.

DISCUSSION

The complete lack of aggression between individuals from the Willcox study site, as well as the high degree of variation in aggressiveness comparing sites was unexpected. Animals from Willcox did not interact aggressively. Because the results were nearly identical for separate years, the responses are very unlikely to be a result of sampling or experimental bias. Animals from Rodeo interacted aggressively and dominated those from Willcox when housed together in Willcox–Rodeo pairs. Rodeo animals attacked Rodeo cagemates at a higher rate than they attacked Willcox cagemates. It appears that aggressive individuals facilitate attacks by their cagemates. The positive correlation in charges between cagemates suggests that charges facilitate charges by cagemates. Thus, the immediate social context influences the level of aggression. That one Willcox individual charged its Rodeo cagemate, after being attacked repeatedly, indicates that Willcox animals are capable of aggressive behavior. Tissues from this animal were included in the mtDNA analysis and found to be indistinguishable from those of the other Willcox and Rodeo *C. uniparens* included in the analysis (Densmore et al., 1989). Variation in the aggressiveness of animals from the Rodeo study area has been documented in other studies dealing with dominance (Grassman & Crews, 1987; Gustafson & Crews, 1981).

Several loci reported as fixed heterozygotes by Dessauer and Cole (1986) were screened in our anaylyis and found to be heterozygous in the 40 specimens surveyed (Aat, Ada, Aldh, Icdh-1, Mdh-1, Mpi-A, two peptidases, Pgm-2, and Sod-A). Further, many of the heterozygote phenotypes displayed a 2:1 ratio of staining intensity on our gels typical of the dosage effect apparent in this and some other triploid parthenogenetic *Cnemidophorus* and the Mdh-1 locus displayed the same 3-allele phenotype (abc) as reported by Dessauer and Cole (1986). Despite the levels of allozyme variability within the Willcox and Rodeo samples, the difference between samples was not statistically significant.

Genetic variation based on protein electrophoresis has been previously reported for *C. uniparens* by Dessauer and Cole (1986). Both protein electrophoresis and restriction endonuclease analysis of mtDNA (Densmore et al., 1989; Moritz et al., 1989; Moritz, personal communication) suggest that the *C. uniparens* populations used in this study are not significantly distinct from each other and may have descended from the same or closely related parental stock. It should be kept in mind that because polyphyletic clones arise from multiple hybrid zygotes, perhaps even from a single hybrid mating (Parker et al., 1989), it should be possible to have multiple hybrid clones which are identical in terms of mtDNA. Although there was no statistical difference between the Willcox and Rodeo populations, eight distinct clones were identified and seven of these were represented in the Willcox sample. Because all but two clones differed at a single locus most of this diversity presumably rep-

resents divergence following hybridization within one or possibly two phyletic clones (Parker et al., 1989). In contrast to the situation at Willcox, the majority of individuals from the Rodeo study site were indistinguishable. Clonal variation at the Willcox study site appears to be high compared to the Rodeo study site. Yet, the animals from the Rodeo study site are more variable in terms of aggressive behavior.

Variation in aggressive behavior observed between *C. uniparens* populations at Rodeo and Willcox, AZ can be accounted for by the frozen niche variation model. Parker et al. (1989) argued that a lack of correlation between color pattern and electrophoretic markers violates an assumption of the frozen niche model; polyphyletic clones which are morphologically distinct also will be genetically "recognizable." Perhaps polyphyletic clones may be genetically distinct but not always recognizable in terms of allozyme variation. In the hermaphroditic killifish, *Rivulus marmoratus*, variation based on histocompatibility tests has been reported among individuals collected in Florida (Harrington & Kallman, 1968; Kallman & Harrington, 1964) whereas allozyme data indicate that genetic homogeneity predominates (Massaro, Massaro, & Harrington, 1975; Vrijenhoek, 1985). In contrast, recent DNA fingerprinting analyses reveal substantial genetic variation and significant mutational distances even among sympatric *R. marmoratus* clones (Turner, Elder, Lauchlin, & Davis, 1990; Turner, Elder, & Lauchlin, 1991). Furthermore, sympatric clones distinguishable using DNA fingerprinting can differ in terms of aggressive behavior (Grassman, unpublished data). If electrophoretic results for individuals are thought of as a phenotypic character like color pattern, one might not predict that these must be correlated across polyphyletic clones. Suites of loosely linked characters should be necessarily related only in so far as they are or evolutionarily, developmentally, and/or functionally related. The frozen niche model takes into account the complexities of the multidimensional niche and predicts that clones should vary phenotypically along multiple axes (Vrijenhoek, 1984). Thus, different clones are likely to be similar in some characters whereas they may vary in others.

In addition to genetic factors, environmental conditions and genotype–environment interactions during development may play some role in the development of aggressive behavior in lizards. Recently, it has been demonstrated that incubation temperatures of lizard eggs influences aggressive behaviors in both males and females (Gutzke & Crews, 1988). Results from the analysis of the monthly and annual data did not seem to explain the observed differences in behavior. The significant month by site interactions indicated that one site was not consistently warmer than the other. Temperature differences between the study sites were small, and although Willcox was warmer than Animas in terms of the monthly analyses, based on annual data Willcox is more like Rodeo than Animas.

In examining the gross climatological data we assumed that this may

correlate with the local environment of the egg during development. However, the possibility that microclimatic differences between study sites could result in differences in aggression between adults cannot be ruled out. While it would be desirable to measure the environment of the nests themselves, the nesting sites for these animals are not known. One might propose that reflectance, moisture content and chemical composition of the soil (the Willcox site is near a large playa), or the kinds of oviposition sites available may influence the development of behavior in these animals. Other factors not related to climate such as density effects on the development of behavior could be important.

Some investigators have argued that individuals of parthenogenetic species may be less aggressive than those of closely related gonochoristic species. Differences in aggressiveness comparing parthenogenetic lizards (*C. tesselatus* and *C. neomexicanus*) and females of gonochoristic *C. sexlineatus* reported by Leuck (1985) were statistically nonsignificant. However, Leuck (1985) concluded that reduced genetic variation in parthenogenetic lizards resulted in reduced aggression (increased altruism). Alternatively, reduced genetic variation may result in reduced heritable variation in behaviors (including altruism) on which natural selection might act. Also, one might expect to find reduced variation in fitness eliminating benefits that would accrue to supposedly altruistic lizards. Species differences not related to reproductive mode (parthenogenetic vs. gonochoristic) and geographic variation must be taken into account in order to determine the effect of reproductive mode on behavior. Thus, it seems unlikely that reduced aggression would apply to parthenogenetic lizards as a general principle.

It must be noted here that a statistically significant correlation between behavioral and biochemical diversity would not demonstrate a causal link between genes and behavior. Conversely, a lack of correlation between allozymes and behavior does not rule out heritability in aggressive behavior. However, a failure to demonstrate a correlation between the genetic analyses and geographic variation in behavior is not meaningless "negative data" but is important information suggesting either that the genetic analyses are not measuring behaviorally relevant genetic diversity (there may be polygenic variation in behavior undetected by the biochemical analyses used), or that clonal genotypes may be quite plastic in terms of behavior. Either way the results raise interesting questions worthy of consideration. In order to demonstrate behavioral variation resulting from multiple hybrid origins, one must identify the genetic basis of the behavior in question. In some gynogenetic fish, for example, ecological and behavioral variation are correlated with variation in certain enzyme markers (Vrijenhoek, 1984). This supports the conclusion that behavior varies among clones. However, in parthenogenetic *Drosophila* individual variation in reproductive output within lineages is as variable as that among different lineages (Crews, Teramato, & Carson,

1985). The present study, taken together with those of Dessauer and Cole (1986) and Crews et al. (1985), indicates that genotypic similarity based on the analysis of a small proportion of structural genes at least in some cases may not accurately reflect the potential genetic basis of variation in behavior, ecology, and reproduction. Laboratory investigations involving *C. uniparens* with documented parental and sibling relationships reared under controlled environmental conditions are needed to explain the relative roles of genes and environment in the development of aggressive behavior in these animals.

ACKNOWLEDGEMENTS

This research was conducted while M. Grassman was a postdoctoral fellow at The University of Texas and supported by NIH NRSA 1F32HD066-8. Additional support for these studies came from MH41770 and NIMH Research Scientist Award 00135 to D. Crews, and from the Department of Biology, Memphis State University.

We would like to thank Y. Morris, J. Lindzey, and J. Rozendaal for assistance in collecting and caring for the animals. W. Gutzke, D. Hillis, R. Semlitsch, and J. Sites and anonymous reviewers provided useful comments on earlier versions of the manuscript. We extend special thanks to the American Museum of Natural History, Southwestern Research Station for their assistance in the field work and ongoing support of our research.

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International Journal of Comparative Psychology, Vol. 5, No. 1, 1991

TEACHING AND RESEARCH IN ANIMAL BEHAVIOUR IN SOUTH AFRICAN UNIVERSITIES: A SURVEY

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ABSTRACT: A qualitative questionaire-based survey of psychology and biology/zoology departments at all 21 universities found in the Republic of South Africa was carried out in 1990 in order to determine how many of them taught and/or conducted research in the subdiscipline of animal behaviour, i.e., either as ethology or comparative psychology or both, and their future plans. Altogether only 10 psychology and 12 biology/zoology departments responded to the questionaire. In addition, a further five psychology departments were contacted via phone or through personal communication. The survey revealed a somewhat disappointing picture with regard to psychology departments—only three of them taught courses in animal behaviour regularly, five taught only small modules on animal behaviour whereas the rest of the departments neither did nor ever planned to do so in the near future. Most psychology departments were of the opinion that the study of animal behaviour was not important at all and consequently only a few of them had conducted or were still conducting some research in the area. In contrast, the picture was a much more exciting one with regard to biology/zoology departments—all of those which had responded, except for one only, had taught courses on animal behaviour in their curricula and had done so for at least a decade. The biology/zoology departments concerned considered animal behaviour to be a relatively important subdiscipline and the majority of them had also conducted or were still conducting some research in the area. Possible explanations for this discrepancy as well as implications thereof for the future of the study of the subdiscipline in South African universities are discussed.

In a survey that I conducted in 1988, which examined the past, present and future status of comparative psychology as a subdiscipline of psychology as taught in psychology departments of universities found throughout English-speaking Black Africa in the following countries: Ghana, Kenya, Liberia, Malawi, Nigeria, Uganda, Zambia and Zimbabwe, I obtained some rather shocking data (Simbayi, 1988). Of about 12 psychology departments that responded to the questionnaire out of the 25 or so different universities in these countries whose participation was solicited, only one had taught comparative psychology on a regular basis

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and considered it as important as other areas of specialization in their undergraduate psychology curriculum whereas the majority considered it neither important nor had any plans whatsoever to offer it in the near future. Nonetheless, two of them did indicate the likelihood of their offering courses in this area in the future pending the availability of funds and/or qualified personnel. The major explanation offered for this state of affairs was that courses in their curricula as well as programmes themselves were chosen primarily on the basis of their social relevance. As a result most them had placed a lot of emphasis on courses and/or programmes which highlighted applied aspects of psychology in such sub-areas as clinical, educational and industrial psychology.

One criticism that could be levelled against this previous survey was that by limiting itself to psychology departments it could not possibly have obtained a clear and fair picture at all because comparative psychology is rarely taught as a course on its own but rather included together with ethology in animal behaviour courses in most universities. For example, most courses follow the layout of such standard textbooks as Alcock's (1979) which combines the two approaches. When this fact is taken together with the apparent existence of a clear demarcation between social sciences on the one hand and natural sciences, particularly biological sciences on the other, one would expect animal behaviour courses incorporating comparative psychology to be taught more in biology and/or zoology departments rather than psychology departments.

The present survey was conducted in South Africa. It was undertaken primarily because to date no such survey appears to have been conducted in that country on this subject. Also in view of the foregoing, the present survey examined the teaching and research in animal behaviour not only in psychology departments but also in departments of biology/zoology. The Republic of South Africa, a country that is very unique in that it is a combination of the first world among the privileged white minority segment of the population and third world among the underprivileged black majority, boasts some 21 universities, a number of which have several campuses. Altogether, they constitute almost a quarter of all the universities found in Africa. Thus, such a study is indeed needed to obtain a broader picture about the status of comparative psychology in Africa outside of the area covered by the previous survey.

METHOD

Questionaires with 10 open-ended questions were sent out at the beginning of March 1990 to heads of departments of psychology and biology/zoology departments at all 21 universities. The heads of departments were asked to either pass the questionaires on to relevant lecturers in their respective departments who taught courses on animal behaviour,

ethology and/or comparative psychology or complete the questionaires themselves if there was no other suitable person who could do so. The respondents were also instructed to return the completed questionaires by the end of the month by post.

Altogether a total of 10 completed questionaires were returned by psychology departments while 12 were returned by biology/zoology departments. In order to increase the number of respondents, additional information was obtained from five other universities via telephone discussions or personal communication, thus bringing the total of psychology departments which responded to 15. In the case of universities with more than one campus, most pooled their information together except for one university which sent two separate completed questionaires. However, these too were pooled for the purpose of analysing the results from the present survey.

RESULTS

Psychology Departments

Of the 15 psychology departments that participated in the survey, only three offered animal behaviour as a full undergraduate course lasting a term: one at second-year level, another at third-year level, and the third one at both levels. Furthermore, research at postgraduate level, namely, masters' and doctorate levels was being offered in two of them whilst the third one had done so previously but had stopped since the mid 1980s following the retirement of the main supporter of the programme in animal behaviour in the department. Of the remainder, five indicated that they taught it as a small component of another full course in general psychology at first-year level whereas the rest (n = 7) did not do so at all. In a way, all psychology departments do teach some aspects of animal behaviour in their first-year courses as part of their modules on the biological basis of behaviour. In particular, topics such as learning and motivation, both of which have a strong animal research background, are covered at standard introductory textbook level.

When asked for how long they had been offering courses on animal behaviour, a total of six out of the eight departments which were offering either a full course or a module stated that they had started doing so for almost three decades since the early 1960s whereas the rest (n = 2) had been doing so for the last decade only. As regards how often these courses/modules were offered, only half of them (n = 4) offered them every academic year whereas the other half (n = 4) did not have a definite timetable.

When asked how important animal behaviour was in their curriculum compared to other sub-areas of psychology, the three departments of-

fering full courses in the sub-area on an annual basis indicated that it was of average importance whereas five indicated that it was not very important and four that it was not important at all. The rest of the departments (n = 3) did not give any response to this question.

When asked what was the main emphasis of the departments in choosing courses for their curriculum, five departments indicated that the main emphasis was to give their students the widest encounter with all major sub-areas of psychology whereas seven revealed that social relevance was the important factor. It is also interesting to note that one department did indicate that both the widest encounter with all aspects of psychology and social relevance were important. The rest of the departments (n = 2) did not respond to this question.

When asked if animal behaviour was taken by both natural and social science students at their university, seven departments indicated that it was taken by both. However, six of the departments revealed that it was taken only by natural science students whereas the remainder (n = 2) did not respond to the question.

As regards whether the person or persons who taught the animal behaviour course/module were specialists, indigenous, and what their level of training was, three departments indicated that the personnel involved were specialists who were indigenous and had trained up to doctorate level in comparative psychology (n = 1) and ethology and primatology (n = 2). In one major university, a total of four lecturers, all indigenous, were involved in teaching courses on animal behaviour and had training in physiological psychology up to masters' level only.

With regards to research, only four departments reported that someone in their department had ever carried out some research in animal behaviour in the past or was still doing so. Of these four, three had trained students in research up to postgraduate level in the past, whereas only two of them were still doing so. All four had also managed to have some of their research findings published in local as well as international journals. The fact that quite a lot of the research findings (in particular those by researchers based in biology/zoology departments who did and still do more research on animal behaviour than those in psychology departments) were published in international journals is most interesting in view of the international academic boycott which was meant to ostracise South African academics over the past two decades or so as a protest against the apartheid policies which were being practised until only last year in South Africa.

Finally, concerning their future plans, only three departments of the seven not currently offering courses on animal behaviour indicated their wish to add a course or module on animal behaviour to their curricula in the near future but all declared that this was very unlikely until either financial resources improved or more pressing human problems had been addressed.

Biology/Zoology Departments

Out of the 12 departments which responded to the questionaire three offered full semester courses on animal behaviour, two offered it in courses lasting one term, i.e., quarter, only, six offered it only as a small component of other full courses ranging from first- to third-year level and only one no longer taught it. Furthermore, up to half (n = 3) of them also offered postgraduate programmes in ethology and/or animal behaviour up to doctorate level.

Of the 11 departments that were teaching courses on animal behaviour six of them had commenced doing so over two decades ago (half of them in the 1960s and the other half in the 1970s) whereas the remainder (n = 5) had started doing so only in the 1980s. The one department that was no longer teaching animal behaviour had done so for over two decades between the 1960s and 1980s and had discontinued due to non-availability of staff with enough expertise to enable them to continue doing so.

Only three of the departments which had responded to the questionaire considered animal behaviour to be extremely important compared with the other areas of specialization which are offered for study in their curriculum. The majority of the departments (n = 7) thought the subdiscipline to be of average importance whilst the remainder (n = 2) considered it as not important at all.

All except two of the departments which had responded to the questionaire indicated that their main emphasis when choosing courses for their curricula was to provide their students with the widest encounter with all the major areas of specialization within biology/zoology. Of the remaining two, one added that social relevance was also important in addition to the reason mentioned above whereas the other one indicated that their criterion was solely relevance for available jobs.

Only three departments indicated that at their universities animal behaviour courses were taken by both natural and social science students. The rest (n = 9) indicated that this was not the case at all. The latter group accounted for the state of affairs by stating that either the two faculties, i.e., natural and social sciences, had overlapping lecture time tables thereby making it impossible for students from either faculty to do courses in the other one or due to the fact that a clear distinction between students in the two faculties existed including entrance requirements and fees. These factors also made it impossible for those in the social sciences to study animal behaviour when it was offered by biology/zoology departments, which are usually in the science faculty.

In eight of the departments animal behaviour was taught by specialists in the field who were all trained up to doctorate levels in subdisciplines such as ethology (n = 3), animal behaviour in general (n = 1), bird behaviour (n = 1), psychology and zoology (n = 1), ecology and physiology (n = 1) and behavioural ecology (n = 1). In one department the lecturer

was trained in mammalogy and reproductive behaviour up to masters' level. In the other two departments which taught animal behaviour courses, teaching was done by nonspecialists. For example, in one such department they had two Ph.D.s, one trained in limnology and the other in acarology, teaching the animal behaviour courses whereas in the remaining one department their two lecturers were trained up to M.Sc. level only, one in general zoology and botany and the other in neurophysiology. With the exception of three expatriates, the majority of these lecturers were all South African citizens.

Finally, regarding research in animal behaviour, all but two of the 12 biology/zoology departments which participated in the survey indicated that some research had been carried out both by staff and postgraduate students in their departments and that some of their findings had been published in both national and international journals. In particular, two of the departments were outstanding in their research output and had also excelled in getting a lot of their research findings published both locally within South Africa and, more importantly, internationally (see also p. 39).

DISCUSSION AND CONCLUSIONS

There are several possible explanations for the observed discrepancy between the prevalence and apparent popularity of teaching and research in animal behaviour in zoology/biology and psychology departments in South African universities. First, the rather strict demarcation between natural and social sciences seen in South African universities as is also the case in many African universities implies that biologically-inclined courses such as animal behaviour will be taught in curricula falling under the faculty of natural sciences, and in particular biology/zoology departments, rather than in psychology departments which fall under social sciences. Second, there is a great difference between the relative importance attached to animal behaviour courses in biology/zoology curricula as opposed to psychology curricula. In particular, biology/zoology departments appeared to place more emphasis on the widest encounter of all major areas of specialization, i.e., sub-fields within their field, unlike most psychology departments which emphasized applied sub-areas of their discipline not only in teaching but also in research. Clearly, the issue of social relevance to the unique South African social context is emphasized in most psychology departments. This state of affairs is further compounded by the relatively strong phenomenological bias which is evident throughout South African psychology in general and in particular its rather rigid subscription to the humanistic approach which advocates that psychological research should be based on humans rather than animals.

On the whole the results obtained from South African psychology departments were more encouraging when compared to those obtained in the previous survey of psychology departments in universities in English-speaking Black Africa (Simbayi, 1988). In particular, relatively more South African universities were offering courses in animal behaviour than was the case in universities in English-speaking Black Africa. Even more encouraging was the fact that training up to postgraduate level was still taking place in at least two of the departments. However, with regard to future plans, most of the South African psychology departments currently not offering animal behaviour courses did not foresee any major changes in their curricula unlike psychology departments in universities in English-speaking Black Africa that indicated that with staffing and/or financial resources permitting they would actually consider offering courses on animal behaviour in their curricula.

On the basis of the foregoing, it may be concluded that the future of animal behaviour in biology/zoology departments is almost certainly guaranteed for the foreseeable future, whereas it is rather bleak in psychology departments. The latter will undoubtedly remain the case until there is a shift from emphasis on courses that are or research that is, either applied or more socially relevant to courses and/or research that allow the widest encounter of all areas of specialization in psychology. This shift also depends on the striking of a fair balance between applied and basic research in psychology departments as is the case with the current practices amongst biology/zoology departments.

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International Journal of Comparative Psychology, Vol. 5, No. 1, 1991

BOOK REVIEW

Attitudes toward wildlife in Botswana, by A. R. Mordi. Garland Publishing Inc., New York, 1991, 200 pp. $46.

"*In the end, we will conserve only what we love, we will love only what we understand, we will understand only what we are taught*" (Baba Dioum). An educated populace is more interested in conservation than is an uneducated one is Baba Dioum's message. Education is not the only factor of importance, though. Richard Mordi's study of attitudes to wildlife and conservation among 555 citizens in Botswana confirms other studies conducted elsewhere in demonstrating that two other correlates are wealth and place of residence. Relatively well-off people and those who live in towns are more interested in conservation and have more positive attitudes about it than do the poor, especially the rural poor. Indeed the rural poor are often adversely affected by wildlife. They don't just see the wildlife on television screens or in magazines; they experience it trampling their fields and taking their livestock. The shopkeeper sitting in his townhouse can afford to like elephants, buffalo, wolves; the small-scale farmer often cannot.

Nevertheless, even among the rural poor, exposure to publicity about wildlife, natural history, and conservation can change opinions. Weber's study of attitudes among rural farmers in Rwanda demonstrates that Dioum is correct in suggesting that knowledge alone, through education, can have a major influence on attitudes, even among the poor. Four years of conservation-oriented publicity in the rural villages around a National Park in Rwanda correlated with a major change in attitude to the Park (Harcourt, 1986; Weber, 1987a,b). The proportion of farmers who saw some value in the Park rose from 49% to 81%; and the proportion who thought that the Park should be degazetted and converted to agriculture dropped from 51% to just 18%.

Being educated, relatively well-off and urban were pervasive and strong correlates of attitudes in Mordi's survey. Another correlate that fairly consistently appeared was gender: men were more knowledgeable and concerned than were women. And cattle-owners tended to differ from those who did not own cattle. These results appear in the book in three forms. We are given the proportion of responses to each of the statements on Mordi's questionnaire that were "agree," "disagree," or "neither"; the mean scores and their statistics for a number of contrasting categories

of the populace; and the results of multivariate statistics which indicate the categories mainly responsible for the differences. I have two different sorts of problems with the results.

One is the nature of the statements on the questionnaire. The statements are not only reversed in content, e.g., lions eat fruit, worms play no part in the ecosystem, the giraffe is not beautiful; they are also sometimes reversed in form. Here I think respondents might have had difficulties. I certainly did double-takes. "A parrot's ability to speak is not fascinating." "What attracts me to a zebra is not its skin markings." If I were in a hurry, distracted by my children, nervous of being asked questions by 'The Government', I can imagine that I would misinterpret some of these statements. Even if we accept the results at their face value, there is still a difficulty. As far as I can see, variables in the middle five tables are presented the wrong way round. High scores should indicate attitudes favourable to conservation, according to the text. However, the data in the tables on 'ecologistic', 'moralistic', 'naturalistic', 'scientistic', and 'humanistic' attitudes show the opposite, so that text and tables contradict one another. When we get to 'neutralistic', 'negativistic' and 'theologistic' attitudes, text and tables once again agree.

There are not many studies of attitudes and their correlates in Third World countries. For this reason alone, this book deserves to be widely read, even if it does come across as the Ph.D. thesis that it is. However, I am afraid that the carelessness in the tables will turn readers away if they notice it, or lead to mistaken perception of the results if they do not. (As an aside, can I ask why the social sciences are so prone to unnecessary neologisms? What is wrong with 'ecological', 'neutral', 'negative', 'religious', or 'scientific' as adjectives, especially when in fact, for example, 'negative', not 'negativistic', is surely the intended meaning? Or do social scientists not wish their work to be understood and used by people from other disciplines, or by those whose first language is other than English?)

In his opening chapter, Richard Morti describes the all important socioeconomic and ecological situation in Botswana. In Botswana, as in many African countries, conservation was and is largely imposed by governmental decree, as opposed to the will of the people. There are few grassroots' equivalents to America's Sierra Club, for example. He is clearly impressed with the government's attitude and efforts, but makes some perhaps exaggerated claims about its preeminence. "More than any other country in Africa, the government in Botswana has gone to extraordinary lengths . . . ." But Tanzania, too, has two wild animals prominent as part of its coat of arms; Tanzania too, and Rwanda, have animals on their banknotes; both have issued many stamps displaying animals of the country; and both have large proportions of their land area gazetted as wilderness Reserves. President Nyerere of Tanzania's Arusha Declaration made a quarter of a century ago is famous among African conser-

vationists for its prescient attitude to conservation of the country's wildlife. I am not denigrating Botswana's conservation efforts, or Mordi's appreciaton of them, but I think it important for people in the industrialised world to realise how deep is the commitment to conservation of many African states and individuals in the face of far more severe socioeconomic problems than we in the West face.

Let me say that I read the book and wrote this review as a conservationist. The results are important, and should reinforce our attempts to persuade some conservation organisations that provision of education, rather than guns, might be the better long-term solution. The book could also be read as a case study by a sociologist or social psychologist, or by anyone else interested in how peoples' socioeconomic background influences their attitudes to anything. As far as I can tell, Mordi wrote for both audiences, conservationist and social scientist. The topic is attitudes to conservation, but he applies Everett Rogers' ideas about diffusion of innovation and Abraham Maslow's about hierarchies of needs to the results. Conservationists have become interested in the field of determinants of attitudes with the realisation that what goes on outside ecosystems is just as important, maybe even more important, than what goes on inside them. The people on the ground charged with management of wilderness have known this for a long time, of course. Nevertheless, up until the last decade or so, conservation was done by biologists and the equivalent of policemen. That is now changing, and many different disciplines are becoming involved in conservation oriented studies, and indeed, conservation oriented development programmes. I hope that this book will stimulate both further study and action.

What action? Richard Mordi's findings emphasise yet again the tragedy of conservation in the Third World. The people of the Third World need to conserve the environment more than the West does, for they are so much more immediately dependent on it. In the USA, when a forest goes, we lose a place to take an afternoon walk; in the Third World, a source of fuel and a barrier against flood and erosion disappears. The poor should benefit most from conservation of Africa, because they depend the most on a healthy environment. And yet it is often the poor who can least afford to adopt the long-term thinking that is so necessary. They cannot cut back today to ensure enough for tomorrow: they do not have sufficient for today. Over much of Africa, wilderness is invaded neither for pleasure, nor for profit, but out of necessity. Only by removing that necessity can the wilderness be saved in the long run.

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To our readers:
I am pleased to announce that the International Society for Comparative Psychology is now publishing its Journal with the assistance of Allen Press, Inc. This issue is being sent to all our subscribers, and we trust that you will renew your subscription so that you will receive the balance of Volume 5, which is now being printed for distribution. Issue #2 will feature a target article by E. A. Salzen on the nature of emotion with commentaries by D. Candland; M. & B. Lewis; J. P. Scott; and P. V. Simonov. Issue #3 presents research reports by M. Delsaut (France); W. Pisula, P. M. Ostaszewski and J. Matysisk (Poland); G. D. Carbines, R. M. Dennis and R. R. Jackson (New Zealand) and P. Roubertoux (France). Issue #4 is devoted to comparative and neuropsychological research in human factors psychology, with papers by D. A. White, D. A. Washburn, R. K. Thomas, and D. M. Rumbaugh and S. L. Williams. Volume 6 will feature the following in addition to research articles: an issue containing previously unpublished documents by V. A. Wagner and B. I. Khotin about the history of comparative psychology in pre-Soviet and Soviet Russia with commentaries by D. Joravsky, N. L. Krementsov, D. B. Malakhovskaya, L. Medacci and V. E. Sokolov and L. M. Baskin; an issue presenting observations by W. Koehler of the behavior of an orang-utan published in English for the first time with commentaries by various investigators of primate behavior; a target article by E. Prato Previde, M. Colombetti, M. Poli and F. C. Spada on animal cognition with commentaries by R. A. Boakes, G. G. Gallup, Jr., J. P. Rossi and C. Robinson; and an issue presenting multiple reviews of the book by R. M. Lerner, Final Solutions: biology, prejudice and genocide.

With the publication of Volumes 5 and 6, my term of office as editor comes to an end. I wish to thank all the authors and reviewers who helped me to bring the first six volumes of the Journal to press, as well as the various editorial assistants who helped us meet deadlines, etc. The Society invites nominations for the position of editor, and these should be sent to me or our Secretary-Treasurer, Dr. Sally A. McFadden, Department of Psychology, University of New Castle, New Castle NSW, 2308, Australia.

In the meantime, I look forward to your comments, suggestions and manuscripts for future volumes.

Sincerely,
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